

SYNTHESIS & INTEGRATION

Beyond the black box: promoting mathematical collaborations for elucidating interactions in soil ecology

ALISON E. BENNETT^{1,†}, KATHARINE PREEDY², ANTONIO GOLUBSKI³, JAMES UMBANHOWAR⁴,
STUART R. BORRETT⁵, LOREN BYRNE⁶, KENT APOSTOL⁷, JAMES D. BEVER⁸, LORI BIEDERMAN⁹,
AIMÉE T. CLASSEN¹⁰, KIM CUDDINGTON¹¹, MARIE-ANNE DE GRAAFF¹², KAREN A. GARRETT¹³, LOU GROSS¹⁴,
ALAN HASTINGS¹⁵, JASON D. HOEKSEMA¹⁶, VOLODYMYR HRYNKIV¹⁷, JUSTINE KARST¹⁸, MIRO KUMMEL¹⁹,
CHARLOTTE T. LEE²⁰, CHAO LIANG²¹, WEI LIAO²², KEENAN MACK²³, LAURA MILLER²⁴, BONNIE OWNLEY²⁵,
CLAUDIA ROJAS²⁶, ELLEN L. SIMMS²⁷, VONDA K. WALSH²⁸, MATTHEW WARREN²⁹, AND JUN ZHU³⁰

¹Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio 43210 USA

²Biomathematics and Statistics Scotland, The James Hutton Institute, Invergowrie, Dundee DD2 5DA UK

³Ecology, Evolution, and Organismal Biology, Kennesaw State University, Kennesaw, Georgia 30144 USA

⁴Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599-3280 USA

⁵Department of Biology and Marine Biology, University of North Carolina-Wilmington, Wilmington, North Carolina 28403-5915 USA

⁶Roger Williams University, One Old Ferry Road, Bristol, Rhode Island 02809 USA

⁷Environmental Review, 925N. Fairgrounds Road, Goldendale, Washington 98620 USA

⁸Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045 USA

⁹EEOB, Iowa State University, Ames, Iowa 50011-1020 USA

¹⁰The Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont 05405 USA

¹¹University of Waterloo, Waterloo, Ontario N2L 3G1 Canada

¹²Boise State University, Boise, Idaho 83725-1515 USA

¹³Institute for Sustainable Food Systems and Plant Pathology Department, University of Florida, Gainesville, Florida 32611 USA

¹⁴National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, Tennessee 37996-1610 USA

¹⁵Environmental Science and Policy, University of California Davis, Davis, California 95616 USA

¹⁶Department of Biology, University of Mississippi, University, Mississippi 38677-1848 USA

¹⁷University of Houston-Downtown, Houston, Texas 77002 USA

¹⁸Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2E3 Canada

¹⁹Colorado College, Colorado Springs, Colorado 80903 USA

²⁰Department of Biology, Duke University, Durham, North Carolina 27708 USA

²¹Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, 110016 China

²²University of Wisconsin, Madison, Wisconsin 53706 USA

²³Department of Biology, Illinois College, Jacksonville, Illinois 62650 USA

²⁴University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599-3280 USA

²⁵The University of Tennessee Institute of Agriculture, Knoxville, Tennessee 37996 USA

²⁶Institute of Agronomic Sciences, University of O'Higgins, Rancagua, Chile

²⁷Department of Integrative Biology, University of California, Berkeley, Berkeley, California 94720-3140 USA

²⁸Virginia Military Institute, Lexington, Virginia 24450-0304 USA

²⁹Northern Research Station, United States Department of Agriculture Forest Service, Durham, New Hampshire 03824 USA

³⁰University of Wisconsin, Madison, Wisconsin 53706-1598 USA

Citation: Bennett, A. E., K. Preedy, A. Golubski, J. Umbanhowar, S. R. Borrett, L. Byrne, K. Apostol, J. D. Bever, L. Biederman, A. T. Classen, K. Cuddington, M.-A. de Graaff, K. A. Garrett, L. Gross, A. Hastings, J. D. Hoeksema, V. Hrynkiv, J. Karst, M. Kummel, C. T. Lee, C. Liang, W. Liao, K. Mack, L. Miller, B. Ownley, C. Rojas, E. L. Simms, V. K. Walsh, M. Warren, and J. Zhu. 2019. Beyond the black box: promoting mathematical collaborations for elucidating interactions in soil ecology. *Ecosphere* 10(7):e02799. 10.1002/ecs2.2799

Abstract. Understanding soil systems is critical because they form the structural and nutritional foundation for plants and thus every terrestrial habitat and agricultural system. In this paper, we encourage increased use of mathematical models to drive forward understanding of interactions in soil ecological systems. We discuss several distinctive features of soil ecosystems and empirical studies of them. We explore some perceptions that

have previously deterred more extensive use of models in soil ecology and some advances that have already been made using models to elucidate soil ecological interactions. We provide examples where mathematical models have been used to test the plausibility of hypothesized mechanisms, to explore systems where experimental manipulations are currently impossible, or to determine the most important variables to measure in experimental and natural systems. To aid in the development of theory in this field, we present a table describing major soil ecology topics, the theory previously used, and providing key terms for theoretical approaches that could potentially address them. We then provide examples from the table that may either contribute to important incremental developments in soil science or potentially revolutionize our understanding of plant–soil systems. We challenge scientists and mathematicians to push theoretical explorations in soil systems further and highlight three major areas for the development of mathematical models in soil ecology: theory spanning scales and ecological hierarchies, processes, and evolution.

Key words: ecological hierarchy; evolution; mathematical model; plant–soil interactions; soil ecology; soil processes; theory.

Received 20 April 2019; accepted 6 May 2019; final version received 12 June 2019. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** bennett.1242@osu.edu

Understanding soil systems, the structural and nutritional foundation for plants and thus every terrestrial habitat and agricultural system, is of utmost importance. Here, we promote mathematical modeling as a tool that can help revolutionize understanding of patterns and processes in soil systems. We argue that true collaborations and effective communication between mathematicians and soil biologists as well as training the next generation of students are needed to address topics that will impact global research challenges such as food security, climate change mitigation, biodiversity conservation, and invasive species eradication.

Theoretical models (qualitative and quantitative, conceptual and empirical) have long been drivers of understanding in population biology, evolution, and ecology (Levins 1966, Weisberg 2006, Pickett et al. 2007, Servedio et al. 2014). The ideal for mathematical models is that they should be applicable or capture the essence of a broad set of situations (general), yield results that match real-life situations (realistic), and produce precise predictions given a specific set of inputs (precision). Levins (1966) argued that it is not possible to maximize all three traits and that there must be trade-offs between them. Despite advances in technology making complex models more manageable, some of these trade-offs

remain (Evans 2012). The consequence of these trade-offs is that while models can be powerful tools to promote understanding and predictability in complex systems, the appropriate model must be selected for the question and system being addressed. However, fewer of these developed models have focused on soil systems (Barot et al. 2007), and in this paper, we advocate for mathematical models as expressions of quantitative theory, be it empirical or conceptual, as powerful tools for increasing understanding of soil systems. We use the term mathematical models to refer to the broad array of models using different mathematical, statistical, and computational approaches to incorporate assumptions about the behavior of a system.

Here we encourage soil ecologists to develop collaborations and expand the use of mathematical models to understand processes, evolution, and interactions within soil systems. This paper is not a comprehensive review of the field of mathematical modeling in soil ecology, but instead a perspectives paper highlighting new directions. While we apply our concerns in this paper to soil systems, many of these questions have been raised in other systems (e.g., food web theory; DeAngelis et al. 1983, Polis and Winemiller 1996, de Ruiter et al. 2006, Moore et al. 2017), and we expect that advance modeling of soil systems will

promote advances in modeling in other fields as well. To that end, the paper is structured to first examine the challenges that may have historically limited modeling in soil ecology, followed by several brief case studies of how mathematical modeling has led to step changes in our understanding of soil systems, and finally, we highlight several avenues by which mathematical models could further our understanding of soil ecology to an even greater extent.

OVERCOME CHALLENGES TO THE APPLICATION OF MATHEMATICAL MODELING TO SOIL ECOLOGY

Until the last few decades, soils were viewed as a unique environment that created challenges for mathematical modeling (Vereecken et al. 2016), and there are still fewer modeling papers in soil ecology journals relative to other fields of ecology and evolution (Barot et al. 2007). However, many of these challenges are either analogous to similar challenges or also exist in other ecological and evolutionary systems and were easily overcome, as described below.

One challenge derived from the fact that soil systems are not homogeneous and contain high spatial variability at multiple scales, driven by complex interactions among soil forming factors. Authors have argued that the great spatial variability and lack of isolated simple species interactions limit our ability to model species interactions in soil systems (Bardgett and van der Putten 2014). In addition to abiotic variability, we know little about the spatial heterogeneity in the distribution of organisms. Structurally, soils are composed of peds (clumps of soil) whose shape and size are influenced by abiotic factors such as pH, soil texture and moisture, or the proportion of sand, silt, and clay; and biotic factors such as organic matter content and the structure and composition of soil biota. These factors interact to influence the transport of water, air, and heat in soils. The stability and structure of peds are also influenced by processes occurring in the rhizosphere including biotic processes such as decomposition and movement, and ecological interactions among soil biota, including soil fauna, bacteria, mycorrhizal fungi, and plant roots (reviewed in Hinsinger et al. 2009, Philippot et al. 2013, Platt et al. 2016, Porre et al. 2016). The pronounced spatial variability among

peds causes complex soil pore structures which create microenvironments that can alter the distribution of organisms and outcome of species interactions which may be perceived to be difficult to include in mathematical models. However, other ecological systems also demonstrate high spatial variability, yet models still provide useful insight and informative predictions in those systems. For instance, spatial variation can alter predator–prey interactions in aquatic systems (Sanford et al. 2003, Sanford and Worth 2009) and modeling showed that spatial heterogeneity can lead to the coexistence of more species than a homogeneous environment (Kneitel and Chase 2004). Within soil systems, stochastic individual-based models have been used to model multiple microbial processes (i.e., physiological and ecological) at multiple levels of different types of soil complexity (Locey et al. 2017). Thus, previous modeling efforts have overcome this challenge, but there is enormous scope for further development of mathematical models accounting for the great spatial variability in soils.

Another challenge is the perception that belowground systems cannot be described using simple models. Much belowground research focuses on communities of organisms or food webs (Bennett 2010, Guttman et al. 2014, Mine et al. 2014, Shi et al. 2016) rather than individual species, especially with the advance of -omics techniques and the study of soil microbiomes (Alivisatos et al. 2015). This research has revealed extensive interdependence among organisms, and that many mutualisms consist of guilds (Stanton 2003) of multiple interacting species (e.g., rhizobia; Lemaire et al. 2015). Models typically focus on the interaction of limited numbers of variables isolated from the rest of their environment. The influence of other effects is assumed to be weak in comparison with the interactions under consideration, justifying their omission from the model. A classic example of this is the Lotka-Volterra model of predator–prey interactions, in which only two variables (one representing the predator and one the prey) are modeled. Differences between model predictions and real-world observations can then illuminate additional factors of importance. Thus, from simple beginnings, models of many systems have evolved to reflect more intricate interactions. For instance, the inclusion of other predators such as wolves improves the fit of

the classic Lotka-Volterra model applied to lynx and hare dynamics (Stenseth et al. 1997). Thus, even simple mathematical models can provide insight into the functioning of richly interacting systems like these and soil systems that may at first sight appear too complex to model.

Historically, the majority of mathematical modeling in soil has focused on organisms of economic interest, such as pathogens of crops (e.g., take-all fungus in winter wheat; Brassett and Gilligan 1989, Heritage et al. 1989, Gilligan and Brassett 1990, Werker et al. 1991, Gilligan 1994, 1995, Gilligan et al. 1994, Colbach and Huet 1995, Bailey and Gilligan 1999, Schoeny and Lucas 1999, Ennaifar et al. 2007, Bailey et al. 2009, Gosme and Lucas 2009, Gosme et al. 2013), and this lopsided emphasis may have limited the use of models to describe processes across both managed and unmanaged systems. Many practical models (calibrated to specific data sets), such as soil-plant-atmosphere models (SPAM), often focus on abiotic instead of biotic factors (reviewed in Manzon et al. 2013). These models make useful predictions for agricultural systems, which are often relatively simple (e.g., fewer plant species, controlled inputs), but may be less informative about processes in unmanaged systems. Also, a heavy focus on applied predictive modeling has limited the range of theoretical questions asked in soil ecology (Bradford and Fierer 2012). For example, there are fewer models of soil predator-prey interactions (Brown et al. 2004, Tully et al. 2005, Neutel et al. 2007, Hohberg and Traunspurger 2009, Kalinkat et al. 2013) than there are models of plant-soil pathogen interactions (see citations above for example of models of the take-all fungus in winter wheat). The development of additional models for managed and natural systems will promote better understanding of all soil systems.

There was also, historically, a perception that mechanisms driving belowground interactions might differ from the mechanisms driving aboveground interactions. However, while scales and organism sizes may differ, many of the same processes that drive aboveground dynamics (e.g., herbivory, predation, mutualisms, pathogen attacks, parasitism) also affect belowground dynamics (Chang et al. 2016). Admittedly, entire categories of organisms (e.g., decomposers) are more common, or at least more easily or

frequently identified, belowground than aboveground. One goal of simplified models is therefore to understand new possible mechanisms; for example, models of belowground functions that include decomposers (or the outcome of their activities; e.g., Moore et al. 2014, 2015a, b). Thus, in some cases, models have already been developed to help determine whether there are differences between the mechanisms driving above vs. belowground processes.

A final challenge is that measurements in soil systems are often problematic. Most soil organisms are difficult to see, identify, and culture, and many types of measurements are destructive. As a result, gathering data to quantify even the most fundamental characteristics or mechanisms, such as fitness or quantifying precise resource exchange values between organisms, is difficult for many soil organisms. Estimating fitness is often the first step to modeling population growth or evolutionary processes and is crucial to understanding how other organisms or abiotic factors influence those dynamics. Above ground, we may be able to estimate the fitness of plants or animals by observing them directly, but belowground collection of even the simplest fitness data may be a challenge. However, new technologies, such as -omics approaches, are leading to a rapidly expanding base of knowledge in soils (reviewed in Alivisatos et al. 2015), which is beginning to address this problem. In addition, the problem of parameter estimation is far from unique to soil systems. This may make predictive modeling challenging, but strategic models (which seek to capture key features of a system rather than the fine detail) can identify which mechanisms and parameters have the greatest influence on the system and can explore suites of possible system dynamics under realistic assumptions. This approach may either allow us to put bounds on key parameter values or on the possible ways in which a system may behave.

NOTABLE INSIGHTS FROM MATHEMATICAL MODELS EXPLORING SOIL ECOLOGY

As highlighted above mathematical modeling has already helped to drive advances in our understanding of belowground systems (Table 1). While these successes are just the beginning, they highlight the many possibilities

for utilizing mathematical models to improve our understanding of soil organisms, interactions, and processes in managed and unmanaged systems.

Here we provide three categories of examples where models have already provided insight into soil systems, and in the following section, we highlight how modeling could help make both incremental and revolutionary shifts in our understanding. A more comprehensive list of approaches can be found in Table 1, but the examples below have been chosen because they provided new insights that allowed a step change in our understanding of soil systems, interactions, and functions.

First, mathematical models can be used to explore systems in which experimental manipulations are impossible. In soil, there are many cases of systems where we cannot manipulate organisms individually, limit resources, or alter interactions, but in principle, such interventions can be modeled. For example, in extensively modeled nutrient mutualisms (e.g., mycorrhizal fungi, rhizobia) we cannot experimentally manipulate how much resource is exchanged between organisms, but we can gain insight from models that identify variables of key interest to test about that resource exchange (Schwartz and Hoeksema 1998, Hoeksema and Schwartz 2003, Kiers and van der Heijden 2006, Kummel and Salant 2006, Kiers and Denison 2008, Landis and Fraser 2008, Cowden and Peterson 2009, Akçay and Simms 2011, Grman et al. 2012, Wyatt et al. 2014, Bever 2015, Jiang et al. 2017). The literature also recommends a number of resources for developing future models in soil nutrient mutualisms (Friesen and Jones 2012, Akçay 2015, Holland 2015). Also, given that a large number of organisms in soil are currently unculturable, we typically cannot experimentally add or remove specific organisms to examine community assembly or function. However, we can model changes in species or functional groups within the community. For example, host-specific changes in soil microbial composition have been connected to the outcome of plant–plant interactions through feedback theory (Bever et al. 1997, Bever 2003, Revilla et al. 2012), which has led to novel insights into forces structuring plant communities (Mangan et al. 2010, Bever et al. 2015, Bennett et al. 2017, Jiang et al. 2017, Teste et al.

2017). There are also more in-depth discussions of modeling in microbial communities in general (Zaccaria et al. 2017). It is also likely that microbial community composition has large effects on decomposition (McGuire and Treseder 2010, Bottomley et al. 2012, van der Wal et al. 2013), but manipulating individual members or species of the decomposer community is virtually impossible. To address this issue, models of decomposition have split the decomposer community into two major functional groups: fungi, which are more effective at breaking down recalcitrant pools of detritus, and bacteria, which are more effective at breaking down labile pools (Moore et al. 2003, 2004, Fan and Liang 2015). These groups have been proposed to form the basis of a compartmentalization of soil food webs into slow and fast energy channels, and theory suggests that the coupling of such channels may serve to stabilize communities by reducing the propensity for oscillations in species densities (McCann et al. 1998, Rooney et al. 2006, Rooney and McCann 2012). Other types of modeling approaches for understanding decomposition have also been used (Manzoni and Porporato 2009, Campbell and Paustian 2015). This particular modeling effort, combined with empirical research, has developed an important paradigm in soil biology: The ratio of fungi to bacteria is thought to be predictive of the function of decomposition in soil systems (Strickland and Rousk 2010, Wall et al. 2010). While the compartmentalization of soil food webs into slow and fast energy channels is now well accepted both by empiricists and modelers, here the modeling by McCann and Rooney showed that these two compartments, while separate, feed into each other creating a consistent decomposition process. This interdependence is impossible to test empirically under all but the most artificial and unrealistic conditions, and thus, this mathematical modeling approach has played a key role in our understanding of decomposition.

Another contribution of mathematical models to exploring systems in which experimental manipulations are impossible is by helping us scale up from the micro- or mesocosm scale at which experiments are typically conducted to larger natural systems about which we need to make predictions. This is one goal of models which incorporate experimentally measured

Table 1. Major areas (and questions within those areas) of soil ecology, theory previously used to address those areas, and potential future theoretical approaches.

Area	Example Questions	Examples of Theory Used	Potential Theoretical Approaches
Hierarchy/Scale			
Ecosystems	How do plants transport compounds from soils to atmosphere?	Soil–plant–atmosphere model (SPAM)	Integrative whole plant physiology that moves across phases (soil–plant–atmosphere)
	What functional groupings predict ecosystem processes?	Food web models incorporating N mineralization and detritus decomposition	Individual-based models Integrate food web and ecosystem models
	What level of taxonomic resolution is needed?		
	What information on belowground organisms is necessary to project how global changes affect agricultural production and natural systems succession?	Niche models using Genetic Algorithm for Rule-Set Prediction (GARP) predict species responses to climate change Stoichiometry	Apply biophysical species range models to soil organisms Apply niche models to decomposers/producers Integrate differential movement rates and biotic niches into spatial models Trait-based approaches Ecosystem multifunctionality Bioeconomic models for restoration
	How can soils be manipulated for restoration/agriculture?	Simulation modeling (not soil focused) Ecosystem engineers (not soil specific) Threshold models Alternative ecosystem states	
	How do small scale soil processes influence net effects across large spatial scales?		Homogenization theory
Communities	How do soil microbes structure or mediate plant community dynamics?	Resource ratio theory R* (resource complementarity) Plant–soil feedbacks Stoichiometry	Integrate resource ratio theory with biotic feedbacks Bipartite networks Ecosystem networks Soil microbe effects on soil structure
	How do soil microbes contribute to community resistance to invasion or disturbance?	Feedback theory Adaptive feedback theory Succession models	Patch model of microbial diversity
	How does species diversity vs species composition drive ecosystem processes?	Portfolio theory Species resource transport/supply rates R* (resource complementarity)	Synergism between microorganisms Add higher order interactions
	What state variables produce useful epidemiological models of disease caused by soilborne pathogens?	Areal dispersal Abiotic predictors Contact spread Population dynamics Ecological Network Analysis	Patch-based plant models Metapopulation models Individual-based models Moment closure models
	How do tri-trophic interactions alter relationships between microbes and plants?	Population dynamics	Incorporate spatial structure
	How common are trophic cascades in soil food webs?	Stoichiometry	Add third trophic level Add connections between consumers of mycorrhizal and saprotrophic fungi Ecosystem networks and Ecological Network Analysis

(Table 1. Continued.)

Area	Example Questions	Examples of Theory Used	Potential Theoretical Approaches
Populations	What is the relative importance of abiotic gradients to community structure?	General Environmental Gradients Climate change (e.g., G'DAY model) Gradient models	Model the effect of incorporating specific soil organisms Model the effect of specific gradients (instead of general) on soil organisms Model how exogenous variability influences coexistence
	Biodiversity/rarity		Extinction models
	What are the implications of the foraging decisions of plants in soils?	Optimal foraging theory Allometry Stoichiometry	3d cellular automata 3d branching process model Model how biota affect scale of foraging/foraging decisions
		Root architecture	NetLogo (type of individual based) models
		Game theory Neighborhood models	
Processes	How do root exudates and rhizosphere gradients affect soil structure?	Markov Chain Monte Carlo	Add temporal structure to patch dynamic models
	How do soil organisms move through soil?	Source-sink models Neighborhood models	Partial differential equation models Random walk models
	Decomposition	CENTURY/DAYCENT	Model feedback and serial loops between discrete pools or across a continuum of states
	What is the relative contribution of symbiotic and non-symbiotic organisms to decomposition?	Simplified CENTURY Plant-microbe competition for nutrients Spatial variation of stoichiometry MEND, CORPSE, MIMICS, SuMMS Social dynamics in and individual-based models	Analytically tractable simplifications
	Aggregate formation	Pedogenesis	Structured models (e.g., spatially structured, biochemically structured, or multi-component models)
Nutrient Cycling	How does the aboveground-belowground biotic community influence soil structure/aggregate formation?	Dynamical models	
	How does soil physical structure/aggregate formation affect restoration efforts?	Network topology Saturated flow models	
	How does aggregate structure influence decomposer and microbial communities?	GPFARM-Range model	Ecosystem network modeling of trophic transfers Metapopulations of nitrogen
	How does soil community structure/AG community influence N cycling?	Discrete model of heterogeneity Equilibrium Chemistry Approximation	Effect of background stoichiometry on discrete nitrogen pools (analogous to chemotaxis in individual microbes)
	How do structures of soil community and AG community influence C storage?	GPFARM-Range model Linear ODE models SWIM CENTURY	Spatial heterogeneity in carbon pools
	How do interactions between decomposers and plants influence nutrient cycles and carbon decomposition?	Nutrient cycle models Spatiotemporal dynamics	Ecological Network Analysis Graph theory Graph theory Finite difference models combining continuous nutrient diffusion with discrete animals and plants

(Table 1. Continued.)

Area	Example Questions	Examples of Theory Used	Potential Theoretical Approaches
Evolution			
Co-evolution	How does co-evolution between plants and soil organisms influence ecosystem processes and community dynamics? Can evolution of soil organisms influence the speed of soil processes?	Recycling loops	Geographic mosaic theory Adaptive dynamics Food web models Genomic models
Mutualisms	What mechanisms stabilize free-living soil mutualisms (e.g., mycorrhizal fungi, rhizobia)? How does bargaining for resource exchange affect population dynamics? How does nutrient exchange between mutualistic partners influence nutrient cycling?	Game theory Biological market models Stoichiometry Partner choice Population dynamics Stoichiometry	Population dynamics Modular models Network modeling Topology altering evolutionary dynamics Uncertainty in link strength
Trade-offs	What selection trade-offs occur within soil systems?		Population dynamics Modular models Uncertainty in link strength

Notes: The abbreviation AG refers to aboveground. Some of the terms used may seem alien to pure empiricists, but they are intended to provide useful key words as a starting point for seeking further information. The full table, including references with examples of these approaches, is presented in the Appendix S1: Table S1.

decomposition dynamics to understand field-level patterns such as CENTURY (Parton et al. 1987, 1993) and other ecosystem models (Agren and Bosatta 1998). A great deal more work is needed in this area (as identified in Table 1). Models can also be run for significantly longer time periods than experiments. Thus, mathematical models can provide insights into soil systems that experimental work cannot and offer testable predictions which may help focus the direction of future experimental work.

Second, mathematical models may be used to test whether hypothesized mechanisms in a system are plausible. A model is constructed and then confronted with data from a natural system. If a model predicts effects seen in nature, either accurately or by capturing key features of the system, then we have evidence that the assumptions of the model (and our understanding of the mechanisms that led to these assumptions) are a plausible approximation of the system. For example, Allison and Folse (Allison 2005, Folse and Allison 2012) produced a population model that assumed decomposers can be relatively altruistic in the sense that they produce extracellular enzymes from which, at high rates of

enzyme production, competitors may benefit. They then built a model of decomposition (as opposed to populations of decomposers) incorporating this assumption, which predicted how nutrient supply and diffusion rate would alter decomposition rates. The output of this model was then compared to a system in Hawaii, and the model explained a relatively large amount of observed variation in litter decomposition (Allison 2012). Thus, we can conclude that the assumption that decomposer production of extracellular enzymes is altruistic is plausible (i.e., it is not inconsistent with these observations). As a result, we now have a better understanding of decomposition systems (likely to be composed of altruistic organisms) than if modeling had not been applied to describe the activity of soil decomposers. There is a growing emphasis in microbial and soil ecology on linking experimental and modeling efforts (Widder et al. 2016).

Third, mathematical models can help us identify the most influential (and hence most important to measure or control) variables in an experimental or natural system. Many processes in soil (e.g., nutrient cycles) are complex, but can

strongly impact both above- and belowground systems. Their complexity can make it difficult to know which variables are the most important to measure to understand a system or a process outcome. For example, which variables should we measure to assess the function or resilience of soil microbial communities (Biggs et al. 2012, Shade et al. 2012)? There are several such examples of model-based variable identification in different soil systems (Larsen et al. 2012). For instance, mathematical modeling has been used to predict when mutualistic mycorrhizal function is likely to decline in agricultural systems and has suggested that arbuscular mycorrhizal (AM) fungal species number is likely the best variable to measure in these systems to predict function (Wyatt et al. 2014). Modeling processes can also allow us to determine how resilient or sensitive soils and soil communities are to change (Bradford and Fierer 2012). For example, a recent modeling approach has shown that the extent of past disturbance in a soil system can influence current responses to environmental change: The more change a community has experienced in the past, the more resilient it will be in the face of new environmental change (Hawkes and Keitt 2015). Thus, the best predictor of responses to environmental change is degree of past disturbance, and this would be the variable to measure in future studies. As a result, mathematical models can shine light into the soil black box by guiding our assessment of soil systems.

The use of mathematical models to affirm or construct new hypotheses about soil processes, identify how soil organisms function and interact, or identify indicator variables to measure in order to assess soil systems will enable us to increase, and may even lead to step changes in, our understanding of soil systems. As the selected examples demonstrate, mathematical modeling has already improved our knowledge of soil systems, and if further employed in this field, they could address a number of important unanswered questions.

PATHS FOR INCREASING THE FUTURE POTENTIAL OF MATHEMATICAL MODELS IN SOIL ECOLOGY

The exemplars described above clearly demonstrate how modeling increases the understanding of soil systems. The philosophy of how to build a

good model and practicalities of model construction have been extensively addressed (Levins 1966, Weisberg 2006, Pickett et al. 2007, Servedio et al. 2014). To challenge scientists and modelers to push theoretical explorations beyond the examples above, we have developed a comprehensive table organized by biological questions within areas of study (elucidated below) with current and potential modeling approaches which may be useful tools with which to build such models (Table 1; Appendix S1: Table S1). Further, here we suggest possible starting points and future directions that may promote greater incremental developments or even revolutionary changes for our understanding of soil ecology. We categorize these possible starting points and future directions into those which test plausible mechanisms, inform about experimentally intractable systems, and identify variables to measure.

The first possible starting point for even greater incorporation of mathematical modeling into soil ecology is the testing of plausible mechanisms. Experimental investigations can reveal different patterns and results in soil biology; however, there may be a suite of possibilities for the interactions behind these patterns and results and mathematical modeling is a useful tool for testing the plausibility of these candidate mechanisms. The manner in which soil microbes affect plant community dynamics is an important open question. Some mathematical models have begun to address this (i.e., resource ratio theory, Cherif and Loreau 2007; R^* , Tilman 1990; plant-soil feedbacks, Bever 1999; and stoichiometry, Miller et al. 2004), but important details remain unaddressed. We argue that combining two of these approaches (resource ratio theory and feedbacks) to model the abiotic and biotic factors that influence plant communities will help elucidate the mechanisms by which soil influences plant communities. Another example is fitness trade-offs, which are thought to be an important constraint on trait evolution in aboveground organisms. However, trait evolution within soil systems has rarely been modeled, and fitness trade-offs are particularly poorly explored. We propose that applying population dynamic models (Bever 1999, Caruso and Rillig 2011) or modular models could advance understanding of evolution within soil systems by testing the plausibility of such mechanisms.

Experimentally intractable soil systems also present excellent opportunities for increased future applications of mathematical modeling. Using geographic mosaic theory, which argues that natural selection varies along a spatial mosaic of patches in which the selection and/or direction of selection varies (Piculell et al. 2008, Andonian et al. 2012), to model soil systems could increase our understanding of co-evolution in a wide array of species interactions in soil. Finite difference models, which are discretization schemes for solving reaction–diffusion type problems and frequently applied in engineering (Abadi and Rahimian 2018, Carrino et al. 2019), geosciences (Shen et al. 2018, Han and Yang 2019), ecology (Potter and Andresen 2002), and evolution (Burgess et al. 2016), could be used to model this theory. We specifically propose the use of finite difference models that combine continuous nutrient diffusion with discrete plants and organisms, and we feel this approach could similarly revolutionize our understanding of how decomposers and plants influence nutrient cycles.

Finally, soil systems are complex and unpacking that complexity is a challenge, but mathematical modeling is a useful tool for identifying key areas of influence. For many reasons, nitrogen cycling is one of the most important processes to understand in soil systems, and previous models explored how soil and plant communities influence this cycle (e.g., GPFARM–Range model; Qi et al. 2012; and a discrete model of heterogeneity, Boswell et al. 2007). We propose that extending current models to metapopulation models of nitrogen would help to link precise points within this cycle to processes of interest. Further, network models could be used to determine the relative importance of coupling among the biogeochemical processes in the nitrogen cycle and determine the species controlling dynamics, similar to efforts in estuarine systems (Hines et al. 2015, 2016). The nitrogen cycle is just one of the complex processes hampering our ability to predict how belowground organisms will influence global change, and a number of models have been developed to help make these predictions (Rastetter et al. 1991). However, applying biophysical species range models to soil organisms (Kearney and Porter 2009) could help to identify which soil organisms predict change and are therefore most important to track over time.

The areas of study used to structure Table 1 are hierarchy/scale, processes, and evolution. Despite the importance of such questions, theory in soil systems has rarely addressed how changes at one hierarchical level or spatial scale influence changes at another. For example, the majority of papers (including those in Table 1) focus on a single ecological hierarchical level such as populations. Hierarchies could be spanned by incorporating the production economy of mutualisms into mathematical models, and multiple spatial scales could be modeled using patch-based models, to add structure to existing models (see Communities in Table 1). Strategic models could also provide qualitative predictions that could be tested across multiple systems, thereby moving beyond simple observations of how interactions between soil organisms produce soil processes.

There are also excellent opportunities to identify when, in soils, variation in spatial and temporal factors is important. Spatial and temporal gradients in the availability of root exudates provide illustrative examples (Table 1). Neighborhood models identified how nematodes and a fungal pathogen responded to patterns in rhizosphere gradients (Anderson et al. 1997, Feltham et al. 2002, Gosme et al. 2013). However, patch dynamic and partial differential equation models could not only further our understanding of these patterns, but could also be applied to a wider range of gradients (Table 1).

Theory is also needed to address how organisms that vary in relative size (e.g., microbes vs. macrofauna) interact with each other. For example, how common are trophic cascades in soil food webs (Table 1)? Do belowground trophic cascades follow the same rules as aboveground trophic cascades? Are the scale differences among organisms proportional to the scale differences observed among aboveground organisms—and does this influence the outcome of trophic cascades?

The second section of the table sets out questions about major processes in soils, focused on ecosystem functions (such as decomposition, aggregate formation, and nutrient cycling). Many of these processes remain a black box, into which we believe theory and modeling will be particularly illuminating. For example, we are still struggling to understand the interplay of biotic and abiotic controls of decomposition. The

development of detailed but complex predictive models such as CENTURY (Parton et al. 1987, 1993) has expanded our understanding of this process, yet many unanswered questions remain. We propose that combining several analytically tractable but simpler models can incorporate multiple dynamics without adding too much model complexity (see Table 1; Forney and Rothman 2014). The power of this approach was illustrated by recent Earth System Models of global carbon cycles that, for the first time, explicitly incorporated microbial communities. These models revealed the importance of microbial processes, especially in scenarios with changing environmental conditions (Wieder et al. 2013). We hope questions in Table 1 will serve as a starting point for developing models of processes that directly link with ecosystem services.

The role of natural selection has rarely been explored in modeling of soil systems, particularly outside mutualistic and pathogenic interactions. A great deal of evolutionary theory has focused on nutritional mutualisms and host–pathogen interactions (see under evolution in Table 1), but for most soil processes (e.g., predation, decomposition), we know very little about the effects of natural selection on soil organisms (Lambers et al. 2009). However, broad brush evolution experiments show that soil systems can adapt to selection pressures in ways that influence plant traits (Bonte et al. 2010, Lau and Lennon 2012, Panke-Buisse et al. 2015). Can changes in land management select for genetic change in bacteria or fungi, and what would be the ecosystem-level implications of such trait evolution? Such questions are more amenable to study than ever before, particularly as next-generation sequencing technologies have increased our ability to identify microbes in soil communities (Alivisatos et al. 2015). Bacterial populations, in particular, have short generation times and respond to selection relatively rapidly (Lau and Lennon 2012, Panke-Buisse et al. 2015). Could such evolutionary responses speed up or slow down soil processes? We propose several modeling strategies that could be used to approach these questions. These include network modeling, topology dynamics, uncertainty in link strength analyses, geographic mosaic theory, and adaptive dynamics (Table 1). To our knowledge,

most of these types of questions have never been addressed empirically or theoretically.

The fields of soil ecology and plant–soil interactions are exciting areas of new discovery for both empiricists and mathematicians. Recent advances in our ability to assess soil microbial communities and identify both organisms and functions provide exciting opportunities for expanding conceptual and mathematical theory and applying this theory to push boundaries in our understanding of aboveground systems. Soils present an incredible opportunity for exploring a wide variety of questions (from micro- to macro-scales and across systems). Here we have focused on how mathematical modeling can contribute to soil ecology, but there are also opportunities for soil ecology to contribute to mathematical modeling. This is a huge opportunity that we have not discussed here. We encourage our fellow scientists to incorporate soil systems into their theory and theory into their soil systems to expand the boundaries of soil science and biology as a whole.

ACKNOWLEDGMENTS

This work was assisted through participation in the “Strategies for the Black Box: Mathematical tools for plant–soil interactions” Investigative Workshop at the National Institute for Mathematical and Biological Synthesis, sponsored by the National Science Foundation through NSF Award #DBI-1300426, with additional support from The University of Tennessee, Knoxville. Alison Bennett and Katharine Preedy were supported by Scottish Government Rural and Environment Science and Analytical Services Division. Antonio J. Golubski was supported by National Science Foundation award DEB-1456927. Jason Hoeksema was supported by National Science Foundation award DEB-1119865. Ellen L. Simms was supported by National Science Foundation award DEB-0645791. The authors would also like to thank Glenn Marion, Christine Hackett, and Philip Smith for comments on the manuscript. Alison E. Bennett, Katharine Preedy, Antonio Golubski, James Umbanhowar, Stuart R. Borrett, and Loren Byrne led the writing process. All authors, except Katharine Preedy, attended the “Strategies for the Black Box: Mathematical tools for plant–soil interactions” Investigative Workshop at the National Institute for Mathematical and Biological Synthesis organized by Alison E. Bennett and James Umbanhowar. All authors contributed to the development of Table 1 and helped in writing.

LITERATURE CITED

- Abadi, R. H. H., and M. H. Rahimian. 2018. Hybrid lattice Boltzmann finite difference model for simulation of phase change in a ternary fluid. *International Journal of Heat and Mass Transfer* 127:704–716.
- Agren, G. I., and E. Bosatta. 1998. *Theoretical ecosystem ecology: understanding element cycles*. Cambridge University Press, Cambridge, UK.
- Akçay, E. 2015. Evolutionary models of mutualism. Pages 57–76 in J. L. Bronstein, editor. *Mutualism*. Oxford University Press, New York, New York, USA.
- Akçay, E., and E. L. Simms. 2011. Negotiation, sanctions, and context dependency in the legume-rhizobium mutualism. *American Naturalist* 178:1–14.
- Alivisatos, A. P., et al. 2015. A unified initiative to harness Earth's microbiomes. *Science* 350:507–508.
- Allison, S. D. 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters* 8:626–635.
- Allison, S. D. 2012. A trait-based approach for modelling microbial litter decomposition. *Ecology Letters* 15:1058–1070.
- Anderson, A. R. A., B. D. Sleeman, I. M. Young, and B. S. Griffiths. 1997. Nematode movement along a chemical gradient in a structurally heterogeneous environment. 2. Theory. *Fundamental and Applied Nematology* 20:165–172.
- Andonian, K., J. L. Hierro, L. Khetsuriani, P. I. Becerra, G. Janoyan, D. Villareal, L. A. Cavieres, L. R. Fox, and R. M. Callaway. 2012. Geographic mosaics of plant–soil microbe interactions in a global plant invasion. *Journal of Biogeography* 39:600–608.
- Bailey, D. J., and C. A. Gilligan. 1999. Dynamics of primary and secondary infection in take-all epidemics. *Phytopathology* 89:84–91.
- Bailey, D. J., N. Paveley, J. Spink, P. Lucas, and C. A. Gilligan. 2009. Epidemiological analysis of take-all decline in winter wheat. *Phytopathology* 99:861–868.
- Bardgett, R. D., and W. H. van der Putten. 2014. Belowground biodiversity and ecosystem functioning. *Nature* 515:505–511.
- Barot, S., M. Blouin, S. Fontaine, P. Jouquet, J.-C. Lata, and J. Mathieu. 2007. A tale of four stories: soil ecology, theory, evolution and the publication system. *PLoS ONE* 2:e1248.
- Bennett, A. E. 2010. The role of soil community biodiversity in insect biodiversity. *Insect Conservation and Diversity* 3:157–171.
- Bennett, J. A., H. Maherali, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. Klironomos. 2017. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* 355:181–184.
- Bever, J. D. 1999. Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecology Letters* 2:52–62.
- Bever, J. D. 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist* 157:465–473.
- Bever, J. D. 2015. Preferential allocation, physio-evolutionary feedbacks, and the stability and environmental patterns of mutualism between plants and their root symbionts. *New Phytologist* 205:1503–1514.
- Bever, J. D., S. A. Mangan, and H. M. Alexander. 2015. Maintenance of plant species diversity by pathogens. Pages 305–325 in D. J. Futuyma, editor. *Annual review of ecology, evolution, and systematics*. Volume 46. Annual Reviews, Palo Alto, California, USA.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology* 85:561–573.
- Biggs, R., et al. 2012. Toward principles for enhancing the resilience of ecosystem services. Pages 421–448 in A. Gadgil and D. M. Liverman, editors. *Annual review of environment and resources*. Volume 37. Annual Reviews, Palo Alto, California, USA.
- Bonte, D., A. De Roissart, M. L. Vandegehuchte, D. J. Ballhorn, T. Van Leeuwen, and E. de la Peña. 2010. Local adaptation of aboveground herbivores towards plant phenotypes induced by soil biota. *PLoS ONE* 5:e11174.
- Boswell, G. P., H. Jacobs, K. Ritz, G. M. Gadd, and F. A. Davidson. 2007. The development of fungal networks in complex environments. *Bulletin of Mathematical Biology* 69:605–634.
- Bottomley, P. J., A. E. Taylor, and D. D. Myrold. 2012. A consideration of the relative contributions of different microbial subpopulations to the soil N cycle. *Frontiers in Microbiology* 3:373.
- Bradford, M. A., and N. Fierer. 2012. The biogeography of microbial communities and ecosystem processes: implications for soil and ecosystem models. Pages 189–200 in D. H. Wall, editor. *Soil ecology and ecosystem services*. Oxford University Press, Oxford, UK.
- Brassett, P. R., and C. A. Gilligan. 1989. Fitting of simple models for field disease progress data for the take-all fungus. *Plant Pathology* 38:397–407.
- Brown, D. H., H. Ferris, S. L. Fu, and R. Plant. 2004. Modeling direct positive feedback between

- predators and prey. *Theoretical Population Biology* 65:143–152.
- Burgess, A. E. F., P. G. Sehofield, S. F. Hubbard, M. A. J. Chaplain, and T. Lorenzi. 2016. Dynamical patterns of coexisting strategies in a hybrid discrete-continuum spatial evolutionary game model. *Mathematical Modelling of Natural Phenomena* 11:49–64.
- Campbell, E. E., and K. Paustian. 2015. Current developments in soil organic matter modeling and the expansion of model applications: a review. *Environmental Research Letters* 10:36.
- Carrino, S., F. Nicassio, G. Scarselli, and R. Vitolo. 2019. Finite difference model of wave motion for structural health monitoring of single lap joints. *International Journal of Solids and Structures* 161:219–227.
- Caruso, T., and M. C. Rillig. 2011. Direct, positive feedbacks produce instability in models of interrelationships among soil structure, plants and arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry* 43:1198–1206.
- Chang, C. H., K. Szlavecz, T. Filley, J. S. Buyer, M. J. Bernard, and S. L. Pitz. 2016. Belowground competition among invading detritivores. *Ecology* 97:160–170.
- Cherif, M., and M. Loreau. 2007. Stoichiometric constraints on resource use, competitive interactions, and elemental cycling in microbial decomposers. *American Naturalist* 169:709–724.
- Colbach, N., and P. Huet. 1995. Modeling the frequency and severity of root and foot diseases in winter wheat monocultures. *European Journal of Agronomy* 4:217–227.
- Cowden, C. C., and C. J. Peterson. 2009. A multi-mutualist simulation: applying biological market models to diverse mycorrhizal communities. *Ecological Modelling* 220:1522–1533.
- DeAngelis, D. L., W. M. Post, and G. Sugihara, editors. 1983. Current trends in food web theory: report on a food web workshop. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- de Ruiter, P., V. Wolters, J. C. Moore, and K. Melville-Smith, editors. 2006. *Dynamic food webs: multi-species assemblages, ecosystem development, and environmental change*. Elsevier, New York, New York, USA.
- Ennaifar, S., D. Makowski, J. M. Meynard, and P. Lucas. 2007. Evaluation of models to predict take-all incidence in winter wheat as a function of cropping practices, soil, and climate. *European Journal of Plant Pathology* 118:127–143.
- Evans, M. R. 2012. Modelling ecological systems in a changing world. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367:181–190.
- Fan, Z. S., and C. Liang. 2015. Significance of microbial asynchronous anabolism to soil carbon dynamics driven by litter inputs. *Scientific Reports* 5:9575.
- Feltham, D. L., M. A. J. Chaplain, I. M. Young, and J. W. Crawford. 2002. A mathematical analysis of a minimal model of nematode migration in soil. *Journal of Biological Systems* 10:15–32.
- Folse III, H. J., and S. D. Allison. 2012. Cooperation, competition, and coalitions in enzyme-producing microbes: social evolution and nutrient depolymerization rates. *Frontiers in Microbiology* 3:338.
- Forney, D. C., and D. H. Rothman. 2014. Carbon transit through degradation networks. *Ecological Monographs* 84:109–129.
- Friesen, M. L., and E. I. Jones. 2012. Modeling the evolution of mutualistic symbioses. Pages 481–499 in J. van Helden, A. Toussaint, and D. Thieffry, editors. *Bacterial molecular networks: Methods and protocols*. Humana Press, New York, New York, USA.
- Gilligan, C. A. 1994. The dynamics of infection by the take-all fungus on seminal roots of wheat: sensitivity analysis of a stochastic simulation model. *New Phytologist* 128:539–553.
- Gilligan, C. A. 1995. Modeling soil-borne pathogens: Reaction-diffusion models. *Canadian Journal of Plant Pathology-Revue Canadienne De Phytopathologie* 17:96–108.
- Gilligan, C. A., and P. R. Brassett. 1990. Modeling and estimation of the relative potential for infection of winter wheat by inoculum of *Gaeumannomyces graminis* derived from propagules and infected roots. *Journal of Phytopathology-Phytopathologische Zeitschrift* 129:58–68.
- Gilligan, C. A., P. R. Brassett, and A. Campbell. 1994. Modeling of early infection of cereal roots by the take-all fungus: a detailed mechanistic simulator. *New Phytologist* 128:515–537.
- Gosme, M., L. Lebreton, A. Sarniguet, P. Lucas, C. A. Gilligan, and D. J. Bailey. 2013. A new model for the pathozone of the take-all pathogen, *Gaeumannomyces graminis* var. *tritici*. *Annals of Applied Biology* 163:359–366.
- Gosme, M., and P. Lucas. 2009. Combining experimentation and modelling to estimate primary and secondary infections of take-all disease of wheat. *Soil Biology & Biochemistry* 41:1523–1530.
- Grman, E., T. M. P. Robinson, and C. A. Klausmeier. 2012. Ecological specialization and trade affect the outcome of negotiations in mutualism. *American Naturalist* 179:567–581.
- Guttman, D. S., A. C. McHardy, and P. Schulze-Lefert. 2014. Microbial genome-enabled insights into plant-microorganism interactions. *Nature Reviews Genetics* 15:797–813.

- Han, T. C., and S. Yang. 2019. Dielectric properties of fractured carbonate rocks from finite-difference modeling. *Geophysics* 84:MR37-MR44.
- Hawkes, C. V., and T. H. Keitt. 2015. Resilience vs. historical contingency in microbial responses to environmental change. *Ecology Letters* 18:612–625.
- Heritage, A. D., A. D. Rovira, G. D. Bowen, and R. L. Correll. 1989. Influence of soil water on the growth of *Gaeumannomyces graminis* var *Tritici* in soil: use of a mathematical model. *Soil Biology & Biochemistry* 21:729–732.
- Hines, D. E., J. A. Lisa, B. Song, C. R. Tobias, and S. R. Borrett. 2015. Estimating the effects of seawater intrusion on an estuarine nitrogen cycle by comparative network analysis. *Marine Ecology Progress Series* 524:137–154.
- Hines, D. E., P. Singh, and S. R. Borrett. 2016. Evaluating control of nutrient flow in an estuarine nitrogen cycle through comparative network analysis. *Ecological Engineering* 89:70–79.
- Hinsinger, P., A. G. Bengough, D. Vetterlein, and I. M. Young. 2009. Rhizosphere: biophysics, biogeochemistry, and ecological relevance. *Plant and Soil* 321:117–152.
- Hoeksema, J. D., and M. W. Schwartz. 2003. Expanding comparative-advantage biological market models: contingency of mutualism on partners' resource requirements and acquisition trade-offs. *Proceedings of the Royal Society B-Biological Sciences* 270:913–919.
- Hohberg, K., and W. Traunspurger. 2009. Foraging theory and partial consumption in a tardigrade-nematode system. *Behavioral Ecology* 20:884–890.
- Holland, J. N. 2015. Population ecology of mutualism. In J. L. Bronstein, editor. *Mutualism*. Oxford University Press, New York, New York, USA.
- Jiang, J., J. A. M. Moore, A. Priyadarshi, and A. T. Classen. 2017. Plant-mycorrhizal interactions mediate plant community coexistence by altering resource demand. *Ecology* 98:187–197.
- Kalinkat, G., U. Brose, and B. C. Rall. 2013. Habitat structure alters top-down control in litter communities. *Oecologia* 172:877–887.
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334–350.
- Kiers, E. T., and R. F. Denison. 2008. Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. *Annual Review of Ecology, Evolution, and Systematics* 39:215–236.
- Kiers, E. T., and M. G. A. van der Heijden. 2006. Mutualistic stability in the arbuscular mycorrhizal symbiosis: exploring hypotheses of evolutionary cooperation. *Ecology* 87:1627–1636.
- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7:69–80.
- Kummel, M., and S. W. Salant. 2006. The economics of mutualisms: optimal utilization of mycorrhizal mutualistic partners by plants. *Ecology* 87:892–902.
- Lambers, H., C. Mougel, B. Jaillard, and P. Hinsinger. 2009. Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. *Plant and Soil* 321:83–115.
- Landis, F. C., and L. H. Fraser. 2008. A new model of carbon and phosphorus transfers in arbuscular mycorrhizas. *New Phytologist* 177:466–479.
- Larsen, P. E., S. M. Gibbons, and J. A. Gilbert. 2012. Modeling microbial community structure and functional diversity across time and space. *FEMS Microbiology Letters* 332:91–98.
- Lau, J. A., and J. T. Lennon. 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proceedings of the National Academy of Sciences of the United States of America* 109:14058–14062.
- Lemaire, B., et al. 2015. Symbiotic diversity, specificity and distribution of rhizobia in native legumes of the Core Cape Subregion (South Africa). *FEMS Microbiology Ecology* 91.
- Levins, R. 1966. Strategy of model building in population biology. *American Scientist* 54:421–431.
- Locey, K. J., M. C. Fisk, and J. T. Lennon. 2017. Micro-scale insight into microbial seed banks. *Frontiers in Microbiology* 7:2040.
- Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466:752–755.
- Manzoni, S., and A. Porporato. 2009. Soil carbon and nitrogen mineralization: theory and models across scales. *Soil Biology & Biochemistry* 41:1355–1379.
- Manzoni, S., G. Vico, A. Porporato, and G. Katul. 2013. Biological constraints on water transport in the soil-plant-atmosphere system. *Advances in Water Resources* 51:292–304.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794–798.
- McGuire, K. L., and K. K. Treseder. 2010. Microbial communities and their relevance for ecosystem models: decomposition as a case study. *Soil Biology & Biochemistry* 42:529–535.
- Miller, C. R., Y. Kuang, W. F. Fagan, and J. J. Elser. 2004. Modeling and analysis of stoichiometric two-patch consumer-resource systems. *Mathematical Biosciences* 189:153–184.

- Mine, A., M. Sato, and K. Tsuda. 2014. Toward a systems understanding of plant-microbe interactions. *Frontiers in Plant Science* 5:423.
- Moore, J. C., R. B. Boone, A. Koyama, and K. Holmfelder. 2014. Enzymatic and detrital influences on the structure, function, and dynamics of spatially-explicit model ecosystems. *Biogeochemistry* 117: 205–227.
- Moore, J. C., P. De Ruiter, K. McCann, and V. Wolters, editors. 2017. *Adaptive food webs: stability and transitions of real and model ecosystems*. Cambridge University Press, Cambridge, UK.
- Moore, J. A. M., J. Jiang, C. M. Patterson, M. A. Mayes, G. S. Wang, and A. T. Classen. 2015a. Interactions among roots, mycorrhizas and free-living microbial communities differentially impact soil carbon processes. *Journal of Ecology* 103:1442–1453.
- Moore, J. A. M., J. Jiang, W. M. Post, and A. T. Classen. 2015b. Decomposition by ectomycorrhizal fungi alters soil carbon storage in a simulation model. *Ecosphere* 6:1–16.
- Moore, J. C., K. McCann, H. Setälä, and P. C. De Ruiter. 2003. Top-down is bottom-up: Does predation in the rhizosphere regulate aboveground dynamics? *Ecology* 84:846–857.
- Moore, J. C., et al. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7:584–600.
- Neutel, A. M., J. A. P. Heesterbeek, J. van de Koppel, G. Hoenderboom, A. Vos, C. Kaldewey, F. Berendse, and P. C. de Ruiter. 2007. Reconciling complexity with stability in naturally assembling food webs. *Nature* 449:599–602.
- Panke-Buisse, K., A. C. Poole, J. K. Goodrich, R. E. Ley, and J. Kao-Kniffin. 2015. Selection on soil microbiomes reveals reproducible impacts on plant function. *ISME Journal* 9:980–989.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51:1173–1179.
- Parton, W. J., et al. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* 7:785–809.
- Philippot, L., J. M. Raaijmakers, P. Lemanceau, and W. H. van der Putten. 2013. Going back to the roots: the microbial ecology of the rhizosphere. *Nature Reviews Microbiology* 11:789–799.
- Pickett, S. T. A., J. Kolasa, and C. G. Jones. 2007. *Ecological understanding: the nature of theory and the theory of nature*, Second edition. Academic Press, Burlington, Massachusetts, USA.
- Piculell, B. J., J. D. Hoeksema, and J. N. Thompson. 2008. Interactions of biotic and abiotic environmental factors in an ectomycorrhizal symbiosis, and the potential for selection mosaics. *BMC Biology* 6: 23.
- Platt, B. F., D. J. Kolb, C. G. Kunhardt, S. P. Milo, and L. G. New. 2016. Burrowing through the literature: the impact of soil-disturbing vertebrates on physical and chemical properties of soil. *Soil Science* 181:175–191.
- Polis, G. A., and K. O. Winemiller, editors. 1996. *Food webs: Integration of patterns & dynamics*. Springer, Boston, Massachusetts, USA.
- Porre, R. J., J. W. van Groenigen, G. B. De Deyn, R. G. M. de Goede, and I. M. Lubbers. 2016. Exploring the relationship between soil mesofauna, soil structure and N₂O emissions. *Soil Biology & Biochemistry* 96:55–64.
- Potter, B. E., and J. A. Andresen. 2002. A finite-difference model of temperatures and heat flow within a tree stem. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 32:548–555.
- Qi, Z. M., P. N. S. Bartling, L. R. Ahuja, J. D. Derner, G. H. Dunn, and L. W. Ma. 2012. Development and evaluation of the carbon-nitrogen cycle module for the GPFARM-Range model. *Computers and Electronics in Agriculture* 83:1–10.
- Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie, and J. D. Aber. 1991. A general biogeochemical model describing the responses of the C and N-cycles in terrestrial ecosystems to changes in CO₂, climate, and N deposition. *Tree Physiology* 9:101–126.
- Revilla, T. A., G. F. Veen, M. B. Eppinga, and F. J. Weissing. 2012. Plant-soil feedbacks and the coexistence of competing plants. *Theoretical Ecology* 6:99–113.
- Rooney, N., and K. S. McCann. 2012. Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution* 27:40–46.
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–269.
- Sanford, E., M. S. Roth, G. C. Johns, J. P. Wares, and G. N. Somero. 2003. Local selection and latitudinal variation in a marine predator-prey interaction. *Science* 300:1135–1137.
- Sanford, E., and D. J. Worth. 2009. Genetic differences among populations of a marine snail drive geographic variation in predation. *Ecology* 90:3108–3118.
- Schoeny, A., and P. Lucas. 1999. Modeling of take-all epidemics to evaluate the efficacy of a new seed-treatment fungicide on wheat. *Phytopathology* 89:954–961.

- Schwartz, M. W., and J. D. Hoeksema. 1998. Specialization and resource trade: Biological markets as a model of mutualisms. *Ecology* 79:1029–1038.
- Servedio, M. R., Y. Brandvain, S. Dhole, C. L. Fitzpatrick, E. E. Goldberg, C. A. Stern, J. Van Cleve, and D. J. Yeh. 2014. Not just a theory—the utility of mathematical models in evolutionary biology. *Plos Biology* 12:5.
- Shade, A., et al. 2012. Fundamentals of microbial community resistance and resilience. *Frontiers in Microbiology* 3:417.
- Shen, W., T. L. Li, P. Li, and J. Guo. 2018. A modified finite difference model for the modeling of flow-slides. *Landslides* 15:1577–1593.
- Shi, S., E. E. Nuccio, Z. J. Shi, Z. He, J. Zhou, and M. K. Firestone. 2016. The interconnected rhizosphere: High network complexity dominates rhizosphere assemblages. *Ecology Letters* 19:926–936.
- Stanton, M. L. 2003. Interacting guilds: moving beyond the pairwise perspective on mutualisms. *American Naturalist* 162:S10–S23.
- Stenseth, N. C., W. Falck, O. N. Bjørnstad, and C. J. Krebs. 1997. Population regulation in snowshoe hare and Canadian lynx: Asymmetric food web configurations between hare and lynx. *Proceedings of the National Academy of Sciences of the United States of America* 94:5147–5152.
- Strickland, M. S., and J. Rousk. 2010. Considering fungal:bacterial dominance in soils – Methods, controls, and ecosystem implications. *Soil Biology & Biochemistry* 42:1385–1395.
- Teste, F. P., P. Kardol, B. L. Turner, D. A. Wardle, G. Zemunik, M. Renton, and E. Laliberte. 2017. Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* 355:173.
- Tilman, D. 1990. Mechanisms of plant competition for nutrients: The elements of a predictive theory of competition. Pages 117–141 in J. B. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, San Diego, California, USA.
- Tully, T., P. Cassey, and R. Ferrière. 2005. Functional response: rigorous estimation and sensitivity to genetic variation in prey. *Oikos* 111:479–487.
- Vereecken, H., et al. 2016. Modeling soil processes: review, key challenges, and new perspectives. *Vadose Zone Journal* 15.
- van der Wal, A., T. D. Geydan, T. W. Kuyper, and W. de Boer. 2013. A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiology Reviews* 37:477–494.
- Wall, D. H., R. D. Bardgett, and E. Kelly. 2010. Biodiversity in the dark. *Nature Geoscience* 3:297–298.
- Weisberg, M. 2006. Forty years of ‘The Strategy’: Levins on model building and idealization. *Biology and Philosophy* 21:623–645.
- Werker, A. R., C. A. Gilligan, and D. Hornby. 1991. Analysis of disease progress curves for take-all in consecutive crops of winter wheat. *Plant Pathology* 40:8–24.
- Widder, S., et al. 2016. Challenges in microbial ecology: building predictive understanding of community function and dynamics. *ISME Journal* 10:2557–2568.
- Wieder, W. R., G. B. Bonan, and S. D. Allison. 2013. Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change* 3:909–912.
- Wyatt, G. A. K., E. T. Kiers, A. Gardner, and S. A. West. 2014. A biological market analysis of the plant-mycorrhizal symbiosis. *Evolution* 68:2603–2618.
- Zaccaria, M., S. Dedrick, and B. Momeni. 2017. Modeling microbial communities: A call for collaboration between experimentalists and theorists. *Processes* 5:19.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2799/full>